

A *PYTHIUM* DISEASE OF GINGER, TOBACCO AND PAPAYA.

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ABOUT three years ago, seedlings of tobacco (*Nicotiana Tabacum*) were found to damp off in large numbers in the seed beds. A few seedlings were incubated in a moist chamber. The next day there was a copious growth of a *Pythium* belonging to the *gracile* group (subgenus *Aphragmium*). It had the following characteristics:—Mycelium branching freely in all the tissues; hyphæ 3 to 8 μ broad, septate in the older branches and frequently with irregular swellings on the hyphæ, sporangia produced in large numbers, lateral, elongated, similar in shape to the hyphæ, slightly swollen at the tip when ripe, without a septum cutting off the sporangial stalk from the parent hypha; zoospores of the usual *Pythium* type; oogonia with oospores not completely filling the cavity, produced on lateral branches and on the hyphal swellings both intra- and extra-matrically. Boiled ants were floated in a dish of water and a piece from the incubated material was put in the dish. On the third day there was a good growth of the fungus on the ants. One of the ants containing the mycelium of the fungus was put in a glucose agar slant. The fungus grew well in this medium and subcultures from it gave pure cultures.

Raciborski¹ found a fungus, which he identified as *Pythium complens* Fischer (which is the same as *P. gracile* de Bary and cannot be distinguished from the earlier *P. monospermum* Prings.), attacking tobacco plants in nurseries which were weakened previously by the attack of *Phytophthora Nicotianæ*

¹ Raciborski, M. *Parasitische Algen und Pilze Java's*, 1 Thiel, p. 8, 1900.

van Breda. He failed to get successful inoculations on healthy tobacco plants. He did not give any details of the fungus, but only mentioned that he did not find any septum cutting off the sporangial stalk. Since *Pythium gracile* de Bary was previously only known as a saprophyte, he suggested for the first time the facultative parasitism of this species.

In July, 1917, seedlings of chillies (*Capsicum annum*) were found to damp off in small quantities. The seeds were got from Bombay. The same *Pythium* was found to be the cause here also.

About the same time, a small ginger plant (*Zingiber officinale*) was found dying in a plot where ginger rhizomes were planted for experiments. The portions above the ground-level were withered. The collar had become very soft and rotten. On examination numerous oospores of a Phycomycete were found in the rotten leaf-sheaths at the collar. The oospores were smooth, thick-walled, and lying loose in the oogonium. Pieces of the rotten stem were incubated in a moist chamber. The next day a copious growth of mycelium with numerous sporangia of a *Pythium* belonging to the *gracile* group developed. Later on oospores also were produced, and these oospores agreed with those found on the plant itself before. This fungus was found to be identical with that causing "damping off" on tobacco and chillies. Pure cultures were taken in the same way as in tobacco.

Butler has previously mentioned¹ that a species identified as *Pythium gracile* Schenk (not de Bary) causes a serious disease of ginger plants near Surat (Bombay). It was pointed out, however, that it is not now possible to be quite certain what fungus Schenk had under study, as he did not describe it fully and there are several allied forms difficult to distinguish from one another. The symptoms by which the disease can be recognized are a withering of the leaves and a softening of the stalks at the collar though not to such a degree as to make them fall over. Specimens preserved in the Pusa Herbarium show that the Surat fungus agrees with that now under consideration. It was not cultivated and no inoculations were carried out.

A form found killing castor plants (*Ricinus communis*) in water culture in India² is perhaps the same.

In 1908-09 McRae³ investigated a disease of ginger in Rangpur (Eastern Bengal) locally called "Jaindhara" and identical with the Surat disease.

¹ Butler, E. J. "An account of the genus *Pythium* and some Chytridiaceæ." *Mem. Dept. of Agric. in India, Bot. Ser.*, I, No. 5, 1907, p. 70.

² Ibid.

³ McRae, W. "Soft rot of ginger in the Rangpur District, Eastern Bengal." *Agric. Journ. of India*, VI, 1911, pp. 139-146.

There also a *Pythium* was found in all diseased plants. Slabs cut out with a red hot knife from the interior of stems that were only slightly diseased, and grown under aseptic conditions, gave pure cultures of the *Pythium* only. He did not carry out inoculation experiments.

McRae studied the field characters of the disease in detail and gives the following account of it :—“ The first outward indication of the disease in the growing crop is a general but slight paleness of the leaves of a shoot, then the tips of the leaves turn yellow, and this yellowing gradually spreads along the leaf towards the leaf-sheath, often more rapidly along the margins. Then the leaf-tissue dies and becomes scarios from the tip, the dead area gradually extending towards the leaf-sheath following in the wake of the yellowish discolouration. The leaves droop and hang down along the stem, till finally the whole shoot becomes dry and withered. Meantime the collar, that part of the aërial stem between the place where it arises from the rhizome and where it emerges from the ground, becomes of a pale, translucent brown colour, and, by the time the leaves are well yellowed, it is very watery and soft so that the whole shoot can easily be lifted off, breaking away at this point though not falling over spontaneously. This soft rot also extends beyond the collar into the rhizome. The rotting is accelerated by the combined action of other fungi and of small eelworms and the larvæ of flies which act as secondary agents. Both the discolouration and softening extend to the whole rhizome, which gradually rots and disintegrates, forming a loose watery mass of putrefying tissue enclosed by the tough rind. The vascular strands lie isolated inside. The roots attached to the affected parts also present the same symptoms.”

During the last few years, numerous cases of an obscure disease like the “ foot rot ” of *Citrus* trees were observed on papaya trees (*Carica Papaya*) in the vicinity of Pusa. It has also been reported from Kathiawar (Western India), Dacca and Burma. Especially during the rainy season of 1909 the disease was very severe in the kitchen garden of this Institute.

The first indication of the disease is the wetting of the bark at the region of the collar and softening of the tissues with a copious exudation of latex which turns brown on coagulation. The patch expands gradually on all sides, sometimes to two feet in length from the base upwards. The tissues inside get discoloured and rotten and give rise to a foul-smelling mass wherein maggots breed in large numbers. The decay travels through the bark into the cambium and thence into the wood, causing rot as it progresses. This rotting continues as long as the weather is damp but is checked by dry weather. The outer bark is then thrown off and a patch is formed, exposing the inner tissue

coated with a black crust, covering up the dried fibrous tissue below. This black crust is composed of the dead plant tissues coloured by the mycelium of a *Diplodia*. The disease is usually active only during the monsoon months, but may then develop with such rapidity as to make considerable progress before the gardener is aware of its presence. It is found chiefly at the base of the trees near the ground-level, but in rare cases it may also occur on the trunk higher up. The disease is most common on trees two or three years old and is rare on young ones. If the attack is very late in the rainy season the trees recover soon; the diseased patch is healed up and the bark only is cast off. Even in extremely severe attacks the tree is not killed rapidly. The effect is often confined for a long time to lessening the yield and size of the fruits. During stormy weather many trees fall over, breaking away at the point of attack. Cultures taken from the coal black crust commonly found in all diseased patches gave almost invariably a fungus belonging to the genus *Diplodia*, which has been identified with some doubt as *Diplodia Papaya* Thuem¹. For some time this fungus was supposed to be the causative organism. Inoculation experiments, however, did not produce the disease artificially under any circumstances.

In 1914, a *Pythium* belonging to the *gracile* group was isolated from the diseased papaya trees, and inoculations with this species did not yield any results. The inoculations were done in the cold weather, and the failure of these may be explained, in the light of the present experiments, as being due to the low temperature and dry weather at the time.

Recently an old tree was found with the typical symptoms of the disease. Many saprophytic fungi and bacteria were found in the diseased patches. Sections from the portion between the healthy and diseased patches revealed the presence of the mycelium of a Phycomycetous fungus in the tissues, and the same kind of mycelium was found under the bark and throughout the diseased patch ramifying freely through the cells. In one place there was a good fluffy growth. The mycelium was hyaline, with thick, granular protoplasm, unseptate in the young hyphæ and irregularly septate in the older. Pure cultures from this mycelium grown on glucose agar proved it to be a species of *Pythium* belonging to the *gracile* group and quite identical with that found on tobacco and ginger. The mycelium in the diseased bark disappears very soon and it is very difficult to detect it in old diseased patches. This explains the failure to find it in the earlier investigations.

¹ Sydow, H. and P., and Butler, E. J. "Fungi Indiæ Orientales, Part V." *Ann. Mycol.*, XIV, 1916, p. 198.

The night after this tree was examined there was heavy rain, and the next morning there was copious growth of the fluffy mycelium on the cut portions of the diseased patches.

Inoculation Experiments.

TOBACCO.

The inoculations with the strain isolated from tobacco were successful only under moist conditions. In those cases where the plants were not covered with bell jars they failed. The inoculated portion of the leaf becomes soft and pale in colour within 24 hours, and the chlorophyll is destroyed. The softening gradually extends to the whole leaf, without being limited by the veins, and leads to total dissolution. Infections on the stem and the growing point produce the same results. In Plate III is a plant drawn on the third day after inoculation. The softening of the infected part is gradually extending to the healthier portions, and the pale-brown, small leaf sticking to the side of the pot shows the wet rot induced as the result of infection from material that ran down off the inoculated leaf.

The mycelium enters through any part of the epidermis and branches freely in the tissues. The hyphæ become constricted before piercing the cell wall. Sporangia are produced only when the infected leaf is floated on water. Irregular swellings on the hyphæ are quite common. Oospores are formed both intra- and extra- matically, the former in larger numbers. Inoculations with this strain on ginger, castor, chilli, papaya, and potato were successful.

TABLE I.

Inoculations with strain isolated from tobacco.

Date	Plant inoculated	Treatment	Place of inoculation	Nature of inoculation	Result	REMARKS
16-9-16	4 tobacco seedlings.	Unwounded and covered with bell jars.	Leaves	Mycelium	3 + 1 -	
„	2 tobacco leaves.	Do.	1 on upper surface. 1 on under surface.	Do.	2 +	
„	Control	Do.	
19-9-16	1 tobacco plant.	Do.	Growing point.	Zoospores in water.	-	Failure perhaps due to drop running off the hairs.

TABLE I—*concl'd.*

Date	Plant inoculated	Treatment	Place of inoculation	Nature of inoculation	Result	REMARKS
19-9-16	1 papaya plant.	Unwounded and covered with bell jars.	G r o w i n g point.	Zoospores in water.	+	
"	1 castor plant.	Do.	Do.	Do.	+	
"	Controls	Do.	
19-12-16	3 tobacco plants.	Do.	Leaves	Do.	3 -	Failure probably due to low temperature.
18-8-17	1 tobacco plant.	Do.	G r o w i n g point.	Mycelium	+	
"	1 ginger plant.	Do.	Do.	Do.	+	
"	1 papaya plant.	Do.	Do.	Do.	+	
"	1 chilli plant.	Do.	Do.	Do.	+	
"	1 castor plant.	Do.	Do.	Do.	+	
"	Sprouting potato tubers.	Do.	Y o u n g sprouts.	Do.	-	
"	Controls	
20-8-17	2 ginger plants.	Do.	T o w a r s d base.	Mycelium	2 +	
"	P o t a t o tubers.	Do.	Y o u n g sprouts.	Do.	-	
27-8-17	2 tobacco plants.	Do.	D i f f e r e n t places.	Mycelium	2 +	
"	2 chilli plants.	Do.	Do.	Do.	2 +	
"	2 castor plants.	Do.	Do.	Do.	2 +	
"	2 papaya plants.	Do.	Do.	Do.	2 +	
"	Controls	
22-9-17	3 papaya plants.	Block removed aseptically and culture inserted. Closed with moist cotton wool.	Base of stem.	Do.	3 +	Weather very damp with drizzling rain at times.

GINGER.

Inoculations with the strain from ginger were carried out on the same host on both wounded and unwounded plants. The results were the same in both cases, except that the action of the fungus was very rapid in wounded plants. The yellowish discolouration of the leaves, the dying of the top shoots, and softening of the collar were quite characteristic. The effect of the infection is seen after about 48 hours.

The hyphæ enter the host through the stomata or any epidermal cell, and swell a little before penetrating (Pl. VI, fig. 4) and also before passing through the cell walls of the internal tissues (Pl. VI, fig. 3). Inoculations with this strain on tobacco and the other plants mentioned above gave successful results.

TABLE II.

Inoculations with strain isolated from ginger.

Date	Plant inoculated	Treatment	Place of inoculation	Nature of inoculation	Results	REMARKS
21-11-16	2 ginger rhizomes.	Unwounded and covered with bell jars.	Rhizome	Mycelium	2 +	
„	1 control	
9-6-17	1 ginger plant.	Unwounded and covered with bell jars.	Rhizome	Mycelium	+	
„	1 Do.	Do.	Leaf-sheath	Do.	+	
„	1 control	Do.	
12-6-17	2 ginger plants.	Unwounded and not covered with bell jars.	Leaf-sheath	Mycelium	2 -	Dry weather.
2-7-17	3 Do.	Do.	Do.	Do.	3 -	Do.
9-7-17	2 Do.	Do.	Do.	Do.	2 +	Weather damp after commencement of monsoon.
„	1 Do.	Wounded and not covered.	Do.	Do.	+	
„	1 control	Do.	
14-7-17	1 ginger plant.	Wounded and covered.	Rhizome	Mycelium	+	
„	1 control	Do.	

TABLE II—*contd.*

Date	Plant inoculated	Treatment	Place of inoculation	Nature of inoculation	Result	REMARKS
28-7-17	1 ginger plant.	Wounded and covered.	Collar	Mycelium	+	
„	1 Do.	Unwounded and covered.	Do.	Do.	+	
„	1 Do.	Wounded and covered.	Rhizome	Do.	+	
„	1 Do.	Unwounded and covered.	Do.	Do.	+	
„	1 control	Wounded and covered.	
7-8-17	1 tobacco plant.	Unwounded and covered.	Leaves	Mycelium	+	
„	1 castor plant.	Do.	Do.	+	
„	1 papaya plant.	Do.	Do.	+	
„	1 chilli plant.	Do.	Do.	+	
„	4 controls.	Do.	
20-8-17	2 ginger plants.	Unwounded and covered with bell jars.	Leaf-sheath	Mycelium	2 +	
„	Potato tubers.	Do.	Do.	-	
25-8-17	Potato boiled.	Covered with bell jars.	Unwounded surface.	Do.	..	Superficial growth only.
„	Potato cylinder cut with borer.	Do.	Wounded surface.	Do.	+	
„	Potato starch exposed by tangential cut.	Do.	Do.	Do.	+	
„	Whole tubers.	Unwounded	Do.	-	
4-9-17	2 young potato plants.	Unwounded and covered.	Young shoot	Do.	2 +	
„	1 control	Do.	

TABLE II—*concl'd.*

Date	Plant inoculated	Treatment	Place of inoculation	Nature of inoculation	Results	REMARKS
4-9-17	1 tobacco plant.	Unwounded and covered.	Young shoot	Mycelium	+	
"	1 control	Do.	
12-9-17	1 papaya plant.	Do.	Petioles and leaves.	Mycelium	+	
"	1 Do.	Do.	Collar and stem.	Do.	+	
"	1 control	Do.	
"	1 potato plant.	Do.	Leafy shoots.	Mycelium	+	
"	1 control	Do.	
"	2 clumps of ginger plants in the field.	Root system exposed and culture placed touching one of the roots and covered with soil.	Roots	Mycelium	-	
17-9-17	1 papaya plant.	Block removed aseptically and culture inserted. Closed with moist cotton wool.	Base of stem.	Do.	+	
"	Same plant as last.	Unwounded. Culture placed on the surface on a different side and covered with moist cotton wool.	Do.	Do.	-	
22-9-17	2 papaya plants.	Do.	Collar	Do.	1 + 1 -	Weather very damp with drizzling rain at times.

PAPAYA.

Inoculations with the strain isolated from this host were quite successful on mature papaya trees, both wounded and unwounded. The wound inoculations were done in the following way:—A piece of the stem was removed under sterile conditions, and part of a culture of the fungus was placed in the cavity. After replacing the piece, the place was covered with a moist pad of

cotton wool. After 48 hours the effect of the fungus was seen. The wetting and softening of the tissues round the seat of inoculation and the exudation of the latex later on were quite characteristic. Penetration of the hyphæ takes place through any part of the plant. The mycelium was seen in the wood tissues and pith. The inner tissues became discoloured brown, and soft. A moist atmosphere greatly helps the spread of the fungus.

TABLE III.

Inoculations with strain isolated from papaya.

Date	Plant inoculated	Treatment	Place of inoculation	Nature of inoculation	Results	REMARKS
15-9-17	1 young papaya plant.	Unwounded and covered.	Collar	Mycelium	Superficial growth only.
"	1 Do.	Wounded and covered.	Do.	Do.	+	
"	1 control	Unwounded and covered.	
17-9-17	1 papaya plant.	Block removed aseptically and culture inserted. Closed with moist cotton wool.	Base of stem.	Mycelium	+	
"	Same plant as last.	Unwounded. Culture placed on the surface on a different side and covered with moist cotton wool.	Do.	Do.	—	
22-9-17	3 large papaya plants.	Block removed aseptically and culture inserted. Covered with moist cotton wool.	Do.	Do.	3 +	Weather very damp with drizzling rain at times.
"	2 Do.	Unwounded. Culture placed on the surface and covered with moist cotton wool.	Collar	Do.	2 +	Do.

Morphology of the Fungus.

The mycelium is composed of much branched hyphæ, sometimes showing false dichotomy, very variable in breadth from 3 to 8μ . Septation occurs very irregularly in old cultures. Irregular swellings on the hyphæ were quite common, when grown on plant tissues or in water culture. In glucose agar the hyphæ are not very broad, and in old cultures they are often septate. In maize and wheat meal the growth of the mycelium is luxuriant and the hyphæ uniform in breadth. In French bean agar the growth of the mycelium is not very luxuriant. On boiled ants the mycelium is very rich in protoplasm and the hyphæ broad. The formation of the sporangia is the same as described in *Pythium gracile*.¹ The sporangial stalk is not cut off by a septum from the parent hypha, but in badly nourished cultures a septum may occur at the base (Pl. V, fig. 6). The irregular swellings on the hyphæ serve as reservoirs of protoplasm, and under favourable conditions sporangia may develop from them. It is not uncommon to find empty cells at the base of the sporangial hyphæ. Sporangia have not been observed on solid media. The development of sporangia and oogonia follows no regular sequence. When cultures are kept in a cool incubator at 21°C ., oospores appear first and later on sporangia. At 30°C . sporangia appear first.

The zoospores are from a few to 35 or more in number in each sporangium. They are bi-ciliate, bean-shaped, slightly depressed at the hilum where the two long cilia are attached, and measure when moving 8 to 12μ , 6 to 8μ in diameter, and when they come to rest 7 to 11μ . They germinate by one or more tubes, which on growing sometimes become septate. No special effect was seen on the discharge of zoospores as a result of lowering the temperature except the delayed formation of sporangia.

The oogonia are formed generally on short lateral stalks but sometimes are intercalary. They are also formed on the bud-like growths developed in the normal mycelium. They are spherical or sometimes slightly longer than broad, thin-walled, hyaline, and measure $18\cdot7$ to 33μ in diameter.

The antheridia may be terminal, or intercalary, or hypogynal. There is generally one antheridium for each oogonium but in rare cases two may be present. The antheridium generally rises from a different branch from that which carries the oogonium but in rare cases from the same branch. At times two antheridia are formed side by side on the same hypha intercalarily, and fertilize different oogonia. The terminal antheridia are club-shaped with a

¹ Butler, *loc. cit.*, p. 68, Pl. I, fig. 6.

pointed beak. The intercalary ones are knob-shaped and pointed. The oospores are round, smooth, hyaline, thick-walled and measure 13.5 to 25.3 μ in diameter. They lie loose in the oogonia and germinate by a germ-tube (Pl. V, fig. 6).

The fertilization is the same as described by Ward.¹

Systematic Position.

None of the species described under the *gracile* group comes very near to the present one, except the species studied by Butler and Ward² and provisionally put under *Pythium gracile* Schenk. However, this species differs in not being an algal parasite. Several inoculations on *Spirogyra* and *Cladophora* gave negative results.

Date	Plant inoculated	Treatment	Nature of inoculum	Result	REMARKS
18-1-18	<i>Spirogyra</i> sp.	Floated in a basin of tap water.	Pythium from tobacco	..	
"	Do.	Do.	Pythium from papaya	..	
"	Do.	Do.	Pythium from ginger from Surat.	..	
"	Do. (control).	Do.	
"	Do. (control).	Floated in a basin of river water	Boiled ants floated in the water to isolate any Pythium already present.		
28-1-18	Do.	Floated in a basin of tap water.	Pythium from papaya	..	
16-4-18	Do.	Do.	Pythium cultures from tobacco, papaya, ginger, mixed together.		
"	<i>Cladophora</i>	Do.	Do.	..	
23-4-18	<i>Spirogyra</i> sp.	Floated in a basin of river water.	Do,		

From *Pythium monospermum* Prings. (*P. gracile* de Bary, *P. complens* Fischer), it differs sharply in the oospore lying quite loose in the oogonium (which may be twice the diameter of the oogonium of *P. monospermum*), and in the antheridia and oogonia usually arising from different branches and not

¹ Ward, H. M. "Observations on the genus *Pythium* (Prings.)." *Quarterly Journal of Microscopical Science*, n. s., XXIII, 1883.

² Ibid.

from the same as is common in the latter. I had *Pythium monospermum* Prings. under observation along with the present one. From *Pythium Indigoferæ* Butl. it differs equally in the characters of the sexual organs. A new name is therefore proposed for the parasite here studied:—*Pythium Butleri* n. sp. (After Dr. Butler, Imperial Mycologist, who first studied the disease on ginger.)

PYTHIUM BUTLERI, n. sp.

Mycelium composed of much branched hyphæ, sometimes showing false dichotomy, the main strands being 3 to 8 μ broad and the lateral ramifications thinner. Irregular swellings quite common on the mycelium, which is septate in old stages. Sporangia lateral, elongated, slightly swollen at the tip. Zoospores few to 35 in number, bean-shaped, bi-ciliate, measuring when moving 8 to 12 μ , 6 to 8 μ in diameter, and after coming to rest 7 to 11 μ . Oogonia lateral or intercalary, spherical or subspherical, thin-walled, and measuring 18 to 33 (average 26 μ). Antheridia terminal or intercalary (when they are usually on a different hypha from that bearing the oogonium) or hypogynal (when they are on the same hypha as the oogonium), knob-shaped. Oospores, round, smooth, hyaline or light yellowish when fully mature, thick-walled, never filling the oogonium completely, 13.5 to 25.3 μ in diameter (average 21 μ). Oospores germinate by a germ tube, not by zoospores. Parasitic on *Nicotiana Tabacum*, *Zingiber officinale*, *Carica Papaya*, *Capsicum annum*, and capable of attacking, when artificially inoculated, *Solanum tuberosum* and *Ricinus communis*.

Remedial Measures.

GINGER.

McRae¹ has given detailed information on the lines of treatment against this disease at Rangpur. The propagation of the disease is chiefly through the use of unhealthy rhizomes for planting, and in rare cases through soil where there is much water-logging. Some seed rhizomes were got from Rangpur, and planted near a crop of local ginger. The Rangpur variety developed the disease and the local one was free. Both had the same treatment. Since the local variety was free, it is evident that the seed rhizomes of the other variety were diseased before planting. So far the disease has been recorded only from Surat (Bombay) and Rangpur (Eastern Bengal). McRae estimated the loss in low lands from 10 to 15 per cent. as

¹ McRae, W. Loc. cit.

against a loss of 5 to 6 per cent. in dry lands. In bad years the whole crop may be destroyed. Butler estimated the loss in a single village near Surat in 1904 at Rs. 10,000. The disease is stated by McRae to be kept in check by adopting the following recommendations :—Burning of all diseased plants, rotation of crops, sowing of healthy seeds, good drainage, and clean cultivation. Some experiments were carried out on the Rangpur Farm¹ to check the disease on these lines and have been successful.

PAPAYA.

Much damage is done in wet seasons. The affected part of the tree should be cut off clean as soon as observed, and the cut parts should be bathed with an antiseptic solution. Sanitary fluid or crude carbolic acid mixed with equal quantity of water and applied with a brush has been found to be very successful. Coal tar can also be applied.

DAMPING OFF OF TOBACCO AND CHILLIES.

Treatment of seed beds with chemicals was not successful. Sterilizing the soil by burning dry grasses on the seed beds prevents the disease.

Note.—After this paper was sent to the press, cross inoculations with papaya strain of the fungus were carried out on ginger, tobacco, chilli and castor plants. All the inoculations were successful. It is quite clear from this that there is no specialization of parasitism among the different strains. [L.S.S.]

¹ "Annual Report of the Agric. Stations in Eastern Bengal and Assam for the year ending 30th June, 1908," p. 30.

Plate II is a reprint of one used to illustrate McRae's paper referred to in the text.